THE AFFINITIES OF THE ECHINOIDEA

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THE recent discovery that the crinoids in their ontogeny increase the number of their ambulacral post-radial ossicles by the interpolation of numerous ossicles (in pairs) between the first two primitive brachials and the radial, forming what are known as "interpolated division series," as well as by the addition of brachials in a linear series at the growing tip of the arm, where only heretofore addition to the number of the brachials was supposed to occur,[1] has shown that in the manner of increase of the number of ambulacral segments there is a close similarity between the crinoids and the echinoids, both groups adding new plates between those already formed and the radials (oculars), whereas in the ophiuroids and the asteroids new plates are added only at the tip of the arms, not, however, at the extreme tip, as in the crinoid arm, but just proximal to a permanent plate; and the question naturally arises, can the commonly accepted view regarding the interrelations of the various classes of the Echinodermata be maintained in the light of the present state of our knowledge?

So long ago as 1821 J. S. Miller remarked on the similarity of an inverted Cidaris to a crinoid, and this similarity was also noticed by Lovén. That this similarity is not superficial but in reality fundamental has become increasingly evident to me during the course of my studies on the echinoderms, and I have now no hesitation in stating that the crinoids and the echinoids have much more in common, and are much more closely related to each other, than either group is to the asteroids or the ophiuroids.

Considering only the external skeleton, we find that, in the crinoids and echinoids (1) the ambulacrals in-

[1] *Proc. U. S. Nat. Mus.*, Vol. 35, No. 1636, pp. 113–131.

crease by the addition of plates proximally between the youngest plate and the radial (ocular); no permanent terminal plate is present; (2) the ambulacral plates always alternate in position; (3) the so-called infrabasals are inconstant (crinoids) or entirely wanting (echinoids and many crinoids); (4) imbrication of ambulacrals is more or less constant; (5) the ambulacrals are on the surface, so that the nerves, water vascular system, schizocœl, etc., are on the inner side, protected by them; (6) there are no definite or constant accessory plates in the ambulacral system; (7) the oral skeleton, when present, can not be directly derived from the ambulacral system; (8) the interambulacral plates are in more or less regular columns; but they always start from a single plate; (9) the interambulacral plates extend laterally outward from the ambulacrals, forming a closed capsule; (10) the plates of the ambulacral system encroach regularly, when at all, upon the peristome, which remains round; (11) the spines are long and usually slender, and are attached to round and prominent spine bosses (present among crinoids in one genus only); (12) the ambulacrals are directly continuous with, and in the same plane as, the radials (oculars): on the other hand, in the ophiuroids and asteroids (1) the ambulacrals increase by the addition of plates distally between the youngest plates and the permanent terminal; (2) the ambulacrals are always opposite each other (a possible exception in certain palæoasteroids); (3) the infrabasals are ontogenetically constant; (4) there is no imbrication of the ambulacrals; (5) the ambulacral ossicles lie deep, so that the radial structures are outside of them; (6) definite and constant adambulacral ossicles or lateral shields are present; (7) there is a peculiar oral skeleton of modified ambulacral plates; (8) the interambulacral plates are in regular rows, starting as some multiple of two; (9) the interambulacral plates enclose more or less the ambulacral plates; (10) the plates of the ambulacral system encroach irregularly upon the peristome, making it more or less sharply stellate; (11) the ambulacral plates

never bear spines; (12) the ambulacrals are not continuous with, nor in the same plane as, the so-called radials or terminals.

This would be sufficient in itself to convince any one that the crinoids and echinoids formed one well circumscribed group, while the asteroids and the ophiuroids formed another similar group, entirely distinct; but the "soft parts" furnish abundant additional evidence leading to the same conclusion.

In the urchins and the crinoids the anus is always well developed and functional, while in the asteroids and ophiuroids it is absent, or, if present, does not serve as an exit for refuse matter; the crinoids and urchins have a large and definite peristome which is circular in shape and more or less filled with dermal plates; in the asteroids and ophiuroids the peristome is very much reduced, stellate and without dermal plates; in the crinoids the ambulacral plates are united by ligaments externally and by two parallel rows of muscle bundles internally; in the echinothurids, which alone among the echinoids have a flexible test, the plates are united by more or less ligamentous connective tissue, and within the test there are five pairs of muscle sheets, inserted along the two outer edges of the ambulacral series; the asteroids and ophiuroids have two pairs of muscles, a dorsal and a ventral instead of one pair and a dorsal (external) ligament. In the crinoids and echinoids the intestinal canal is narrow, tubular, without marked sac-like expansions, and always lies in coils of which there may be as many as four; in the asteroids and ophiuroids the digestive system runs direct from the mouth to the anus (when present) without convolutions, but has sac-like widenings, and may have branched radial outgrowths. In the crinoids and the echinoids the gonads are connected with the axial organ in the young, but not in the adult; in the asteroids and ophiuroids they are connected with the axial organ throughout life. In the echinoids and crinoids the pseudo-hæmal system is closed on all sides; in the asteroids and ophiuroids it connects by means of numerous

small apertures with the body-cavity, and, at one point in the pseudo-hæmal ring, with the axial sinus. A blood vascular system is doubtfully present in the ophiuroids and asteroids, but well developed in the echinoids and crinoids. In the echinoids the axial sinus surrounding the stone canal, originally a part of the cœlom, is in open communication with the ampulla into which the madreporite opens. This is comparable to the condition in the crinoids where the madreporic pores open into the body cavity more or less opposite the openings of the stone canals, but is quite different from the condition found in the asteroids and ophiuroids.

Having now shown that the crinoids and the echinoids are closely related, it remains to be seen how an homology may be drawn between the skeletal elements of the two. This is not nearly so difficult a performance as might appear at first sight. The primibrachs of a crinoid represent the first four ambulacral plates of an urchin, which have slipped in between each other so as to lie in a single row; in this single row of four plates the second has disappeared, as shown by the synarthry,[2] while the third and fourth have united to form an axillary. All the plates in the crinoidal post-radial series up to the third brachial of the free arm represent the ambulacral series of the urchin; the long and tapering crinoid arms from the third brachial onward are homologous to the auricles and apophyses of the urchin, which have become turned outward instead of inward, have become interiorly united, and have increased enormously in length. The crinoid stem is the central (sur-anal) plate of the urchin; originally free, the crinoids first became sessile through simple attachment by the central dorsal plate; this gradually increased in thickness, becoming a thick stalk, like that of Holopus; later, owing to the increasing length, fractures were developed transversely, and finally the long jointed crinoid stem resulted.

It has been urged, from their radiate structure, that the echinoderms were primarily fixed; but I can not see

[2] AMERICAN NATURALIST, Vol. 43 (October, 1909), pp. 577–587.

why the octopus could not be assumed to have been descended from stalked ancestors along the same lines. It seems to me that the echinoderms are rather like the bivalve molluscs or the crustacea which contain both free and fixed types, the former in the great majority. The crinoids are the only recent fixed echinoderms; but in the fossil crinoids, as Lang pointed one in Marsupites and I independently showed in Uintacrinus, there are forms which exhibit no evidence of ever having been attached; in fact the evidence is quite the other way. In these forms the centrale may be, instead of the centro-dorsal, really the dorso-central, in which case we should get an interesting homology with the echinoids.

The association of the holothurians with the echinoids, and hence with the crinoid-echinoid stem, seems to me to be abundantly justified. The following classification of the echinoderm groups is proposed as showing the interrelations of these groups better than any of the synopses previously published.

Phylum ECHINODERMATA

I. Subphylum ECHINODERMATA HETERORADIATA.
  A. Pelmatozoa.
    1. Crinoidea.
    2. Cystidea.
    3. Blastoidea.
  B. Ovozoa.
    1. Echinoidea.
  C. Vermiformes.
    1. Holothuroidea (Bohadschoidea).

II. Subphylum ECHINODERMATA ASTRORADIATA.
  A. Ophiobrachiata.
    1. Ophiuroidea.
  B. Stellarides.
    1. Asteroidea.

In this table the sequence of groups must not be taken to represent a phylogenetic line; in no class of animals is a phylogenetic sequence more difficult of conception than in the echinoderms. While the heteroradiate echinoderms are, judged by ordinary standards, more perfect than the astroradiate, judged from the echinoderm point of view solely, they can not be considered so well developed as the latter.